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ACADÉMIE EUROPÉENNE
INTERDISCIPLINAIRE
DES SCIENCES

INTERDISCIPLINARY EUROPEAN ACADEMY OF SCIENCES

Lundi 2 octobre 2017:
à 17 h à la Maison de l'AX, 5 rue Descartes 75005 PARIS

Conférence (*en anglais*) du Pr Pier Francesco FERRARI ,
Directeur de Recherche au CNRS,
Institut des Sciences Cognitives Marc Jeannerod, Université Claude Bernard, Lyon:
"*Construction d'un Cerveau Empathique* "

Notre Prochaine séance aura lieu le lundi 6 novembre 2017 à 17h
5 rue Descartes 75005 PARIS

Elle aura pour thème

Assemblée générale annuelle de l'AEIS

Académie Européenne Interdisciplinaire des Sciences
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TABLE DES MATIERES

Prochaine séance : lundi 6 novembre 2017

Assemblée générale annuelle de l'AEIS

ACADEMIE EUROPEENNE INTERDISCIPLINAIRE DES SCIENCES
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5 rue Descartes 75005 PARIS

Séance du Lundi 2 octobre 2017 /Maison de l'AX 17h

La séance est ouverte à 17h **sous la Présidence de Victor MASTRANGELO** et en la présence de nos Collègues Gilbert BELAUBRE, Gilles COHEN-TANNOUDJI, Alain CORDIER , Jean-Felix DURASTANTI, Françoise DUTHEIL Claude ELBAZ, Michel GONDRAN, Irène HERPE-LITWIN, Edith PERRIER, Jacques PRINTZ, Jean SCHMETS , Michel SPIRO, Jean-Paul TEYSSANDIER , Jean-Pierre TREUIL .

Etaient présents en tant que visiteurs Jean BERBINAU administrateur du lycée Saint Louis et du Collège Stanislas , Denise PUMAIN Professeur émérite à l'Université Paris I Panthéon Sorbonne (Géographie physique, humaine et sociale) et René PUMAIN chercheur à l'INSEM.

Etaient excusés :François BEGON, Jean-Pierre BESSIS, Jean-Louis BOBIN, Bruno BLONDEL, Michel CABANAC, Alain CARDON, Juan-Carlos CHACHQUES, Daniel COURGEAU, Sylvie DERENNE, Ernesto DI MAURO, Vincent FLEURY, Robert FRANCK, Jean -Pierre FRANÇOISE, Dominique LAMBERT, Valérie LEFEVRE-SEGUIN, Gérard LEVY, Antoine LONG, Pierre MARCHAIS, Claude MAURY, Anastassios METAXAS, Jean-Jacques NIO, Alberto OLIVIERO, Marie-Françoise PASSINI, Pierre PESQUIES, Alain STAHL, Mohand TAZEROUT , Jean VERDETTI.

I.   . **Présentation de notre conférencier Pier Francesco FERRARI par Victor MASTRANGELO**:

Pier Francesco FERRARI, est titulaire d'un doctorat d'état de l'Université de Parme en Italie en Psychopharmacologie et comportement (1997) et de formations post doctorales à l'Université de Tufts USA en Neurosciences (1997-1998) et à l'Université de Parme en Italie en Neuroscience et Cognition (1998-2002).

Il est actuellement **Directeur de Recherche au CNRS** à Lyon-Bron à l'Institut des sciences cognitives Marc Jeannerod (UMR5229) rattaché à Institut des sciences biologiques (INSB). Il est également Professeur adjoint (Adjunct Professor) à l' Université du Maryland, Programme USA Neuroscience and Cognitive Science et Pofesseur invité (Visiting Professor) à l'Université de Reading en Grande Bretagne. Il a jusqu'en 2016 exercé en tant que Professeur associé à l'Université de Parme en Italie .Il a dans ce contexte encadré 8 chercheurs post doctorants, et 14 doctorants**.**

Concernant **ses publications**, il est l'auteur de deux ouvrages publiés, 2 publications générales, et d'une centaine de publications dans des ouvrages à comité de lecture , 15 chapitres de livres.... Il est également **reviewer** de 45 publications scientifiques à comité de lecture et de fondations de recherche et éditeur associé de la revue Behaviour , membre du comité éditorial de PLoS One, Frontiers in Neurosciences, Frontiers in Comparative Psychology, Scientific Reports. Il a été **conférencier** dans une centaine de conférences internationales. Il est membre de diverses sociétés savantes telles que "Society for Neuroscience", "International Society of Behavioral Neuroscience"....

Il dispose pour son laboratoire de neurophysiologie d'équipements sophistiqués tels que des enregistreurs à canaux multiples, des caméras à imagerie thermique. Sa recherche est conséquemment **subventionnée** par les gouvernements français et italien, la communauté européenne et par le NIH.

II. Conférence du Pr Pier Francesco FERRARI

Résumé de la conférence:

Construction d'un cerveau empathique

L'empathie est la capacité de comprendre et de partager les états internes des autres. C'est un phénomène multidimensionnel complexe qui implique de nombreux processus fonctionnels incluant la reconnaissance de l'émotion, la contagion émotionnelle aussi bien que des aptitudes cognitives plus complexes dans lesquelles la réponse aux émotions des autres n'implique pas un partage des mêmes états internes, facilitant ainsi des réponses altruistes et prosociales. Les investigations pratiquées aux niveaux neurophysiologiques ont démontré qu'un mécanisme crucial de l'empathie est développé par un mécanisme d'action-perception dans lequel le système moteur active des représentations partagées entre l'observateur et l'agent qui manifeste une réponse émotionnelle/affective. Ainsi, être témoin de l'émotion des autres n'est jamais passif, mais c'est un processus actif de prise en miroir ou de simulation de la même expérience affective. Certaines formes d'empathie ont été décrites chez d'autres primates et animaux, indiquant que l'empathie est un ancien héritage évolutif probablement apparu pour soutenir des échanges intersubjectifs dans des espèces très socialisées et faciliter ainsi la cohésion de groupe.

Ces dernières années, l'empathie a été explorée à partir d'une perspective développementale aussi bien chez les primates humains et non humains. Les études sur les effets des expériences sociales précoces entre le nourrisson et celui qui en prend soin ont souligné l'importance des périodes de sensibilité précoces dans la construction de l'expérience affective des autres. Les perturbations dans les expériences sociales précoces pourraient conduire à des divergences de correspondance entre les représentations internes de l'expérience des autres et l'expérience affective réellement observée. Je vais explorer certains de ces sujets en vue d'établir quelques explications théoriques concernant le rôle critique du couplage d'action-perception neural dans l'émergence d'un cerveau empathique et dans la construction du partage d'expériences et de représentations .

Un compte-rendu détaillé sera prochainement disponible sur le site de l'AEIS , http://www.science-inter.com

Annonces

I. **Quelques ouvrages papiers relatifs au colloque de 2014 '' Systèmes stellaires et planétaires- Conditions d'apparition de la Vie''** -
   – Prix de l'ouvrage :25€.
   – Pour toute commande s'adresser à :

   Irène HERPE-LITWIN Secrétaire générale AEIS
   39 rue Michel Ange 75016 PARIS
   06 07 73 69 75
   irene.herpe@science-inter.com

II. **L'ouvrage cité ci-dessus est accessible gratuitement sur le site**:

http://www.edp-open.org/images/stories/books/fulldl/Formation-des-systemes-stellaires-et-planetaires.pdf

III. Pour la prochaine assemblée générale seuls les membres titulaires ayant acquitté leur cotisation seront habilités à voter.

Documents

Pour compléter l'intervention du Pr   Pier Francesco FERRARI nous vous proposons:

p.07 : issu du site https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5110041/, un article intitulé "Empathy: Gender effects in brain and behavior" publié dans Neuroscience & Biobehavioral Reviews. doi: 10.1016/j.neubiorev.2014.09.001 en 2014 co-signé par Pier Francesco FERRARI.

Empathy: Gender effects in brain and behavior

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Abstract

Go to: ⌄

Evidence suggests that there are differences in the capacity for empathy between males and females. However, how deep do these differences go? Stereotypically, females are portrayed as more nurturing and empathetic, while males are portrayed as less emotional and more cognitive. Some authors suggest that observed gender differences might be largely due to cultural expectations about gender roles. However, empathy has both evolutionary and developmental precursors, and can be studied using implicit measures, aspects that can help elucidate the respective roles of culture and biology. This article reviews evidence from ethology, social psychology, economics, and neuroscience to show that there are fundamental differences in implicit measures of empathy, with parallels in development and evolution. Studies in nonhuman animals and younger human populations (infants/children) offer converging evidence that sex differences in empathy have phylogenetic and ontogenetic roots in biology and are not merely cultural byproducts driven by socialization. We review how these differences may have arisen in response to males' and females' different roles throughout evolution. Examinations of the neurobiological underpinnings of empathy reveal important quantitative gender differences in the basic networks involved in affective and cognitive forms

of empathy, as well as a qualitative divergence between the sexes in how emotional information is integrated to support decision making processes. Finally, the study of gender differences in empathy can be improved by designing studies with greater statistical power and considering variables implicit in gender (e.g., sexual preference, prenatal hormone exposure). These improvements may also help uncover the nature of neurodevelopmental and psychiatric disorders in which one sex is more vulnerable to compromised social competence associated with impaired empathy.
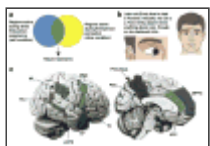
Keywords: Ontogeny, Gender, Sex, Contagion, Mimicry, Prosocial, Helping, Emotion, Mirror neuron system, Development, Evolution

1. Introduction   Go to: ☑

Empathy – the ability to understand and share in the internal states of others – is a complex, multidimensional phenomenon that includes a number of functional processes, including emotion recognition, emotional contagion, and emotion priming (for recent reviews, see Decety and Jackson, 2006; Singer, 2006; Walter, 2012), as well as the abilities to react to the internal states of others, and to distinguish between one's own and others' internal states (e.g., Tomova et al., 2014). From the perspective of evolutionary and developmental biology, empathy's purposes, in both humans and nonhuman animals, can be broadly divided into two categories: *Promoting prosocial, cooperative behavior, and understanding or predicting the behavior of others* (Smith, 2006).

Empathy has been studied from many perspectives (Davis, 1980; Decety and Moriguchi, 2007; Zaki and Ochsner, 2012). For example, social psychology has examined the manifestations of empathy within moral reasoning and social behaviors like mimicry (e.g., Sonnby-Borgström, 2002). In economics, studies have considered empathy's effects on decision-making (e.g., Beadle et al., 2012; Loewenstein, 2005; Ferrari, 2014). Cognitive neuroscience studies of empathy, on the other hand, are mainly divided into two lines of research, one focused on preconscious mechanisms which underlie/facilitate sharing (and mimicry) of others' behaviors and internal states (we will refer to it as *mirroring*); the other line of research is focused on a conscious, deliberative process through which inferences can be made about others' bodily and affective states, beliefs, and intentions (often called *mentalizing*) (Keysers and Fadiga, 2008; Zaki and Ochsner, 2012). These two aspects of empathy can be roughly mapped onto *affective* (or pre-reflective) and *cognitive* (reflective) empathic predispositions, respectively (Smith, 2006). Affective empathy is associated with activity in frontoparietal, temporal, and subcortical regions classically associated with movement, sensation, and emotion, while neural systems involved in cognitive control and decision-making – such as the cingulate, prefrontal, and temporal areas – are often activated during tasks requiring cognitive empathy (see Fig. 1) (Zaki and Ochsner, 2012).

Fig. 1
Neuroscientific approaches to studying experience sharing and mentalizing. (a) The experimental logic underlying first-person perception studies of experience sharing. The blue circle represents brain regions engaged by direct, first-person experience **...**

How are these two primary modes of empathizing – cognitive empathy and affective empathy – related? While affective empathy involves pre-reflective processes, humans seem nevertheless capable of consciously and unconsciously modulating it. Furthermore, humans are capable of internally evoking emotions, behaviors, and sensations of an absent other, or even of ourselves at another point in time. We are also capable of inhibiting our internal states and reflexive responses to others. Indeed, numerous studies have shown that mirroring is modulated by numerous contextual factors, such as social distance, status, trustworthiness, group membership, and attention (Bernhardt and Singer, 2012; Gu and Han, 2007; Guo et al., 2012; Hogeveen et al., 2014; Lamm et al., 2007; Liew et al., 2011; Loggia et al., 2008; Singer et al., 2006), and is controlled by systems involved in cognitive empathy (Spengler et al., 2010). Conversely, some authors propose that mentalizing and social decision-making may employ information derived from mirroring (Iacoboni et al., 2005; Obhi, 2012; Zaki and Ochsner, 2009) (Fig. 2).

Fig. 2
Proposed relationship between mentalizing and mirroring processes and their accompanying brain systems.

Recent studies suggest that a large portion of the ability to read intentions derive from pre-reflective mechanisms for processing biological motion (Obhi, 2012), and studies of empathic accuracy have shown that accurately discerning the internal states of others, as well as inferring intentions from observed behavior, relies on the interaction between mirroring and mentalizing processes (Liew et al., 2011; Zaki and Ochsner, 2012). There is also evidence that our immediate affective responses to others' pain and distress can increase prosocial decision-making (Christov-Moore and Iacoboni, under revision; Hein et al., 2010; Masten et al., 2011; Ma et al., 2011; Smith, 2006). Indeed, it is likely that, without the interactive participation of both modes of empathizing, social interactions would be impaired, potentially impacting the health and wellbeing of the individual as well as those around him/her (Gallese, 2003).

While we now associate the mentalizing system with decision-making, musing about others etc., this system may have arisen in part as a form of contextual control for mirroring. In our view, this seems likely for two reasons: compared to the mirroring system, both the mentalizing system's cognitive functions and the brain areas that underlie mentalizing (i.e., temporal and prefrontal cortices), (1) developed more recently in our evolution and (2) are the last to mature during ontogeny (Preston and De Waal, 2002). Furthermore, neural systems associated with mentalizing have been implicated in the control of behavioral mirroring (mimicry) (Spengler et al., 2010). Indeed, recent evidence from our group (Christov-Moore and Iacoboni, under revision) suggests that *mirroring areas and mentalizing areas exist in interaction rather than as independent systems*. Rather than just using the mirroring system when we view others in pain, feeling emotion, or having fast social interactions that are typically thought to bypass mentalizing (Bohl and van den Bos, 2012), and using the mentalizing system when we need to consciously make decisions in a social setting, guess the beliefs and intentions of others, or take another person's perspective, *we may use both at all times*. Obviously, one system may take the lead over the other, depending on the situation's demands.

This larger dynamic system formed by the interactions between mirroring and mentalizing may allow individuals to revisit past experience and behavior, predict the consequences of their own behaviors, both for themselves as well as for others, and to selectively share in the behavior and affective states of others in response to context (such as common group affiliation).

An understanding of empathy would be incomplete without a consideration of individual differences. Popular conceptions of *gender*[1] – defined here as reflecting both self-identification (i.e., females, males) as well as biological classification (i.e., female, male) – contain expectations about empathy and empathic behavior, many of which have been borne out by extant research. However, empathy and gender remain difficult to define, in part because the disciplines that study them use distinct and often non-overlapping methods and terminology. While this difficulty is not something we can address in this article, we should keep it in mind when considering the evidence reviewed here.

In reviewing gender differences in empathy, we propose to address two questions: first, *how deep do gender differences in empathy go?* Cultural and societal effects on gender differences are most pronounced in explicit measures in which adults are asked to describe themselves or produce a behavior which is clearly related to "empathy" or "sympathy" (Eisenberg and Lennon, 1983; Gleichgerrcht and Decety, 2013). However, meta-analyses examining gender and sex differences in empathy provide results supporting fairly stable gender differences across a broad range of measures (e.g., Cohn, 1991; Eisenberg and Lennon, 1983; Feingold, 1994; Hall, 1978, 1984; Hoffman, 1977; O'Brien et al., 2013; Thompson and Voyer, 2014; although, for null results see Lamm et al., 2007). Additionally, empathy has developmental precursors in early infancy (Alexander and Wilcox, 2012; McClure, 2000) as well as evolutionary precursors in other social animals (Preston and De Waal, 2002). Indeed, there is considerable overlap between empathetic behaviors demonstrated in young humans early in development and in nonhuman animals. Thus, in addition to examining implicit measures of empathy, we can look to developmental and evolutionary precursors of empathy for a more complete view of sex differences.

The second question this review will address is the nature of empathy itself, that is, what are its *core biological and neural underpinnings?* More specifically: are individual differences in cognitive and affective subcomponents of empathy independent or tightly integrated (or somewhere in between)? Are individual differences in the behavioral manifestations of empathy, such as social competence or prosocial behavior, due to differences in low-level processes like emotional reactivity, or higher level functions like spatial reasoning or theory of mind (ToM)? Which components of empathy emerge first during ontogeny, and does each component accomplish a specific proximate or ultimate function throughout development? To what extent, and in what way, is empathy modulated and controlled by higher cognitive functions? As recent cognitive neuroscience reviews have suggested (Zaki and Ochsner, 2012), the relationship between the principal components of empathy, as they are currently studied, remains unclear. Although several scholars agree that emotional and cognitive component of empathy underpin a broad range of empathic responses, a global concept of empathy remains elusive, and this is in large part due to a lack of cross-talk among the disparate fields that study it. Studying gender differences in empathy might provide insights to understanding empathy by observing whether such differences covary across different measures. For example, if we were to find consistent gender differences in both affective empathy and prosocial behavior, but less consistent differences in cognitive empathy, we might infer that affective empathy drives prosocial behavior.

To address these issues, we structured this review into four parts. First, we will examine the evolutionary precursors of empathy. Then, we will review gender differences related to the psychological and behavioral processes associated with empathy. Sex differences in empathy will be also evaluated from an ontogenetic point of view. Lastly, we will review evidence suggesting that gender differences assessed at behavioral and psychological level are supported by specific neural substrates.

2. Evolutionary precursors of empathy Go to: ☑

In the last few decades, as outlined above, it has become evident that empathy is not limited to the cognitive manifestation of the capacity to take the perspective of another, putting oneself in others' shoes. Instead, empathic responses are often revealed by immediate responses of the body (e.g., Levenson and Ruef, 1992), suggesting that the brain mechanisms mediating such responses are often devoid of cognitive efforts (Shamay-Tsoory, 2014; Shamay-Tsoory et al., 2009).

Empathy should therefore be better understood as a multilayered phenomenon. There is general agreement that one of the most basic forms of empathy is a fast, stimulus-driven response that aligns the motor behavior of the observer and the observed (Carr et al., 2003; Zaki and Ochsner, 2012; Preston and De Waal, 2002; De Vignemont and Singer, 2006). This fast response appears to be the basis of *emotional contagion*, in which emotions spread from individual to individual through mimicry, for instance, when someone smiles and observers immediately do the same (Lakin et al., 2003; McIntosh, 2006). A number of studies show that vocalizations, postures, and movements are often mimicked without awareness (e.g., Hatfield et al., 1992; Chartrand and Lakin, 2013). For example, as Darwin (1872) wrote:

> When a public singer suddenly becomes a little hoarse, many of those present may be heard, as I have been assured by a gentleman on whom I can rely, to clear their throats; but here habit probably comes into play, as we clear our own throats under similar circumstances." (p. 34)

As we review below, most of these phenomena are likely related to the activity of a mirror mechanism through which the observation of others' actions or emotions activates motor programs corresponding to observed actions.

Recent work has demonstrated that such emotional and behavioral responses, including sensitivity to conspecifics' distress, are common in the animal kingdom as well (e.g., monkeys: Nagasaka et al., 2013; pigs: Reimert et al., 2013; rats: Ben-Ami Bartal et al., 2014; mice: Sanders et al., 2013; Mancini et al., 2013; Palagi et al., 2009). Empathetic behavior appears particularly strong in social species with prolonged parental care, such as mammals and some birds, in which there are reports of behaviors that are indicative not only of sensitivity to others' emotional states, but also of the presence of some basic forms of empathy (Gonzalez-Liencres et al., 2013; de Waal, 2008; Edgar et al., 2011). In some species, the bond between individuals is expressed through sophisticated emotional channels that have been shaped through a long natural history. For example, capacities to cooperate, to support conspecifics during conflicts, and to provide comfort to social partners in distress have been widely described in primates and other animals (e.g., elephants: Plotnik and de Waal, 2014; chimpanzees: Romero et al., 2010).

These phenomena imply that a type of affective channel between individuals may be involved in some species' social relationships. In support of this hypothesis, recent empirical studies in gelada baboons have demonstrated that the speed and frequency of rapid facial mimicry ([Fig. 3](#)) were higher among individuals with strong bonds, such as mothers and their infants ([Mancini et al., 2013](#)).

[Fig. 3](#)

An example of rapid facial mimicry of play face in two juvenile gelada baboons (taken by PFF).

Interestingly, in bonobos yawn contagion appears stronger between kin and friends than with unrelated individuals ([Demuru and Palagi, 2012](#)), thus suggesting that emotional contagion is affected by the quality of the relationship and by the affective attunement between individuals. Recent work in humans supports this hypothesis by demonstrating that the rate of contagion is greater in friends and kin compared to strangers and acquaintances ([Norscia and Palagi, 2011](#)).

Although a number of studies have documented empathic or proto-empathic behaviors in the animal kingdom (for reviews, see [Edgar et al., 2012](#); [Panksepp and Panksepp, 2013](#)), few studies have tested whether there are sex differences in empathy. This is primarily due to the fact that animal studies, like many human studies, often have small samples or samples of only one sex, therefore not allowing such comparisons. Such studies are important because they can shed light on the evolutionary mechanisms that were selected to facilitate empathy in some individuals, thus leading to individual differences in empathic predisposition ([de Waal and Suchak, 2010](#)). We review below a small number of studies in animals that suggest higher levels of empathy in females than males, a motif that seems to recur in the human literature as well.

2.1. Emotional contagion: Yawning, facial mimicry, and pain

One behavioral manifestation of empathy is *mimicry*, including facial mimicry ([Niedenthal et al., 2010](#); [Davila-Ross et al., 2008](#)) and contagious yawning ([Platek et al., 2003](#); [Campbell et al., 2009](#)), both of which occur in human and nonhuman animals ([Figs. 3](#) and [4](#)).

[Fig. 4](#)

A yawn response of one chimpanzee during presentation of a yawn videotape (from [Anderson et al., 2004](#)). The chimpanzee (named Ai) watches a yawn on the screen (top left), starts to yawn as the stimulus yawn ends (top right), continues to yawn (bottom **...**

Gelada baboons exhibit rapid facial mimicry, with the highest levels of mimicry occurring during mother–infant play ([Mancini et al., 2013](#)). In terms of sex differences, female baboons, compared to males, exhibit stronger and more specific matching of yawn types ([Palagi et al., 2009](#)). This may reflect stronger bonds among females, compared to males. Interestingly, in this species, females form coalitions, have long-

lasting relationships, and share in infant care, thus supporting each other through alloparental care. If the dominant male dies or is replaced, the females do not disperse but remain assembled in the group. It has been proposed that this form of social organization may favor the capacity of females to be emotionally tuned to one another (Palagi et al., 2009). In bonobos, yawn contagion is strongest when the model is a female (Demuru and Palagi, 2012). This finding is reminiscent of data in humans showing greater empathy directed at females than males (Bryant, 1982; Olweus and Endresen, 1998).

A number of species can use the emotional expressions of others to guide their own behavior (e.g., Morimoto and Fujita, 2011); however, few studies have examined whether there are sex differences in sensitivities to conspecifics' emotional expressions. For example, when viewing a conspecific in pain, the pain-associated behaviors in the viewer (e.g., writhing) can indicate the amount of empathy. Recent work in rodents suggests females have greater sensitivity to other's pain compared to males. In mice, for example, both males and females appear to increase their writhing when viewing a familiar individual in pain (Langford et al., 2006). However, when paired with an unfamiliar individual, males, but not females, show a decrease in their writhing, suggesting less sensitivity toward the pain of the unfamiliar mouse (Langford et al., 2006). These data seem to be in accord with studies in humans suggesting that males tend to have their empathetic responses influenced more by contextual cues compared to females (Brehm et al., 1984; Ickes et al., 2000; Singer et al., 2006).

2.2. Consolation and prosocial behavior

Consolatory behavior, that is, providing comfort to victims of aggression or individuals who are otherwise upset, appears to be widespread throughout the animal kingdom. This behavior has been documented in great apes (e.g., chimpanzees: de Waal and van Roosmalen, 1979; bonobos: Palagi et al., 2004; gorillas: Cordoni et al., 2006), canines (e.g., dogs: Cools et al., 2008; wolves: Palagi and Cordoni, 2009), corvids (e.g., ravens: Fraser and Bugnyar, 2010; rooks: Seed et al., 2007), and, most recently, elephants (Plotnik and de Waal, 2014). Most of these studies, however, had insufficient sample sizes to allow for examination of sex differences. Although sex differences in these studies were rarely examined, in chimpanzees, female bystanders were more likely to console distressed individuals than males (Romero et al., 2010), and in lowland gorillas, immature females offer more frequent consolatory contact than males (Cordoni et al., 2006).

One important aspect of empathetic behavior is whether individuals come to the aid of others in need and attempt to help them. While this phenomenon has been well described in nonhuman primates (e.g., capuchins: Drayton and Santos, 2013; orangutans: Liebal et al., 2014), it is also present – perhaps somewhat surprisingly – in rodents. For example, female mice were more likely than male mice to approach cagemates who were restrained and in pain, compared to an unaffected cagemate (Langford et al., 2010). Females did not, however, approach unfamiliar mice in pain. Stress may trigger females, but not males, to increase their affiliation toward familiar social partners, as well as improving their general empathic tendency, a phenomenon known as the "tend-and-befriend" response (Taylor et al., 2000; also see Bull et al., 1972; Tomova et al., 2014). Another study in rats found that females, compared to males, were faster and more likely to release a trapped cagemate (Ben-Ami Bartal et al., 2011). This form of helping behavior occurred even when rats were not allowed social contact after releasing the cagemate, and even when offered a food reward. The study suggests that rats, especially females, may behave in intentionally prosocial ways, without training or reward, and act prosocially even when prosociality decreases food intake (i.e., having to

share food with cagemate). Similarly, adult female rats are more likely than male rats to approach 50-kHz vocalizations –appetitive calls that occur during rough-and-tumble play, associated with positive affect, and which may serve as contact calls (Seffer et al., 2014; Willadsen et al., 2014).

Sex differences in other animals have also been observed. Jackdaws – a large-brained corvid species – were given the option of either choosing a prosocial action, in which both the actor and the recipient received food, or a selfish action, in which only the actor received food (Schwab et al., 2012). Female jackdaws were more likely than males to behave prosocially, while males were more likely to behave selfishishly. In another study where males were not tested, female chimpanzees demonstrated spontaneous preferences for prosocial rewards, as opposed to selfish rewards (Horner et al., 2011). Chimpanzee mothers and their offspring exhibit flexible helping behaviors, providing partners with tools to accomplish their goals (Yamamoto et al., 2012). Female chimpanzees are also more likely than males to share food with individuals with whom they have strong affiliative bonds (Eppley et al., 2013).

2.3. Sensitivity to others in play and caregiving

Sex differences in caregiving can emerge early in development, as evident in studies of play behavior. Studies investigated how individuals manipulate objects, such as dolls, that traditionally are handled differently by boys and girls. In chimpanzees, juvenile females are more likely than males to carry sticks as if they were infants (i.e., cradling sticks in their arms), while males are more likely to use sticks to hit one another (Kahlenberg and Wrangham, 2010). Other studies show that while female play more often involves caring for another individual (e.g., pretended baby), male play does not (e.g., Goldberg and Lewis, 1969; Hines, 2008). Indeed, in vervet and rhesus monkeys, males played longer with wheeled toys and females played longer with dolls and plush toys (Hassett et al., 2008; Alexander and Hines, 2002), similarly to human children (Pellegrini and Smith, 2005). This may occur due to different selective pressures on males and females because of their different behavioral roles, with females more often being the primary caretakers of offspring (Alexander and Hines, 2002), helping to practice relevant skills for survival and reproduction (Smith, 2010). However the proximate mechanisms underlying these different preferences remain largely unknown (for a review, see Williams and Pleil, 2008). In Old World monkeys, females demonstrate more interest in infants, engage in more play parenting throughout their juvenile years, and spend more time handling infants than males (Geary, 1998; Maestripieri, 1994; Pryce, 1995). Similarly, while male dolphins engage in more solitary object-based play, females engage in more social play (Greene et al., 2011). If play functions to prepare males and females for different social roles, then sex differences in play would only be present in species in which males and females have different roles. For example, in grey wolves (*Canis lupus lupus*) males and females have similar social roles (e.g., collectively rear offspring, cooperative hunting), and exhibit no differences in social play (Cordoni, 2009), but in domestic dogs (*Canis lupus familiaris*) sex differences in play have been observed (Pal, 2008; Ward et al., 2008). For example, in domestic dog puppies, when males played with females they initiated more offensive interactions (attack and pursuit) and more self-handicapping behaviors than females, while females were found to initiate play more with other females (Ward et al., 2008). Play may be important in helping individuals to learn to interpret emotional signals of others (LaFreniere, 2011), a skill which is foundational to empathy.

2.4. An evolutionary ancient instinct to care for offspring

It is possible that parental care is the ancient root from which more complex forms of empathy have emerged (Preston, 2013). However, in several species, beyond mammals and birds, parents show complex forms of energy-demanding and potentially life-threatening parental care, such as in spiders, cephalopods, fishes, frogs, and reptiles (Trumbo, 2012). It is unclear whether empathy is a key factor in motivating such behaviors, given that, in most of these cases, parent intervention is not triggered by the needs of the offspring (which could reveal sensitivity to others' internal states), but rather by external danger stimuli activating defensive behavioral responses (Rosenblatt, 2003). For example, in some species of spiders the young remain with the mother for an extended period, during which time the mothers provide food and defense (Yip and Rayor, in press). Mammals evolved more complex behavioral strategies to cope with immature offspring, possibly because such prolonged maternal care is necessary to facilitate offspring weaning and independence (Olazábal et al., 2013).

During the periods that precede and follow birth, mothers in all mammalian species experience changes in their physiology, anatomy, and behavior (Olazábal et al., 2013). In most mammalian species, in terms of energy costs, mothers invest more in each offspring, compared to fathers (Martin and MacLarnon, 1985). In some species, like chimpanzees, a mother usually gives birth to one infant every five years, and keeps nursing for years, during which time the infant's only source of food is the mother's milk (Tutin and McGinnis, 1981). Unlike humans, females of most Old World monkeys and apes rear their infants alone and largely without the collaboration of other females (Hardy, 1976; Rogers and Davenport, 1970). The mother–infant relationship in primates is unique, characterized by the infant constantly clinging, mother–infant embracing, and prolonged ventro-ventral contact (i.e., contact in which the infant clings to the front of the mother in old-world monkeys and apes; e.g., Manning et al., 1994; Maestripieri, 1994).

Primates' long period of altriciality (i.e., dependence on the mother for food, safety, etc.) may have produced a series of changes in females' capacity to detect and respond adaptively to newborns' signals and needs, that may impact the quality of mother-infant relationships, and ultimately, infants' long-term health. First, mothers must synchronize their own biological cycle and daily activities with the infants' basic needs (e.g., being fed periodically and for a long period of time). Given their extended period of need, infants evolved a system to communicate their internal states to their mothers, based on their own needs and goals. In addition, the infants' process of gaining independence is long and the early stages of environmental exploration are mediated by the presence of the mother who provides oversight, food and protection. This process is commonly framed in terms of 'attachment' (Chisholm, 1996), a framework that provides a theoretical underpinning of the bond between infants and caregivers (Bowlby, 1969). One of the central concepts in attachment theory is the proximity to the mother (Maestripieri, 2001, 2003). For example, in old world monkeys, apes, and humans, the mother plays a key role in the evolution of attachment because mothers play an active role in breaking and making contacts with their infants as they become independent. Furthermore, in primates, the mother–infant communication system relies on a complex combination of visual signals, vocalizations, and gestures. The evolved facial communication system of primates is particularly suitable to express emotions and to externalize internal state. Continuous ventro-ventral contact allows for face-to-face interactions, as mothers and infants are already facing one another (Matsuzawa, 2007). These face-to-face interactions have profound effects on mothers' biology and psychology, in terms of mothers' capacity to evaluate

the infants' distress, to anticipate dangers, to re-establish contact with offspring when it is lost, and to reduce the infant's agitation or fear associated with separation (Maestripieri, 2003).

Females, as the primary caretakers of the young infants, may have evolved adaptations to be sensitive to nonverbal expressions, as such sensitivities may have increased infant survival (Babchuk et al., 1985; Hampson et al., 2006). According to the *Primary Caretaker Hypothesis*, males did not experience this same selective pressure, and therefore this may account for sex differences in emotion recognition and empathy. Indeed, maternal sensitivity and a healthy attachment influence infants' health and immune functions (Goldberg, 2000). Human newborns are also sensitive to facial signals and mother–infant interactions are characterized by a rich-repertoire of face-to-face interplays with a clear temporal structure (Feldman, 2007; Stern, 1977; Trevarthen, 1979). During these shared moments mothers provide important social inputs to infants, which are critical for infants' social and cognitive development (Trevarthen, 1998; Nagy, 2006). More recently it has been shown that similar patterns of face-to-face interactions are present in monkeys and apes, during which mothers produce a variety of facial expression to the infants, exaggerating the gestures and accompanying them with vocalizations (Ferrari et al., 2009; Maestripieri and Wallen, 1997; Matsuzawa, 2007).

Might this primary caretaker selective pressure account for sex differences in empathy? An attempt to answer this question may be possible through future studies that compare species with higher degrees of paternal care – such as in siamangs, tamarins, marmosets, titi monkeys, and owl monkeys – with species with lower degrees of paternal care. Sex differences in empathy should be predicted by the species-typical degree of relative paternal and maternal care. For example, in titi monkeys and owl monkeys, the fathers are the primary carriers of the infants, and may carry infants for up to 90% of the time (Fernandez-Duque et al., 2009). In titi monkeys, in fact, infants actually prefer their fathers to their mothers (Mendoza and Mason, 1986).

To summarize, the evidence thus far is consistent with the idea that *selective pressures shaped females' anatomy, physiology, and neurobiology to facilitate sensitivity to infants' internal states and resultant nurturing behavior*. Hence, sex differences in foundational aspects of empathic behavior may derive from a common evolutionary history of maternal care.

3. Behavioral and psychological gender differences in humans   Go to: ☑

3.1. Emotion recognition, priming, and emotion contagion

In humans, the ability to recognize other people's emotions varies among individuals (Martin et al., 1996). Throughout the non-verbal perception literature there appears a consistent pattern of interindividual differences: a female advantage in nonverbal emotion recognition, in both visual and auditory modalities (Hall, 1990; McClure, 2000; Schirmer et al., 2007; for recent reviews, see Kret and De Gelder, 2012; Stevens and Hamann, 2012; Thompson and Voyer, 2014). Though an extensive review of these studies is outside of the scope of the present review, we will focus on a few key areas of emotion recognition related to empathy, including emotion conveyed through body language, emotion contagion, and socioemotional priming.

Studies report that facial expression recognition skill for briefly presented faces – which therefore must be processed using rapid, prereflective strategies – is positively correlated with self-reported empathic concern ([Davis, 1983](#)). In contrast, facial expression recognition skill for expressions presented for longer lengths of time – therefore allowing more cognitive-based strategies – is correlated with self-reported cognitive empathy and social understanding ([Lawrence et al., 2004](#)). Therefore, *both types of empathy, emotional and cognitive, are related to individual differences in skills for identifying other people's emotions* ([Besel and Yuille, 2010](#)).

Females are faster and more accurate than males in recognizing facial expressions (e.g., [Babchuk et al., 1985](#); [Hampson et al., 2006](#); [Thayer and Johnson, 2000](#)). There is also a small but growing literature on gender differences in the ability to recognize *emotional body language*. The point-light display method allows for the study of biological motion, such as body language, and consists of displaying little spots of light at various points on the target's body, which then move when the target moves, on a dark background, and therefore reflect the motion of a specific movement (e.g., walking, running, jumping), while removing all other cues ([Johansson, 1973](#)). Females, compared to males, appear to be faster ([Alaerts et al., 2011](#)) and more accurate ([Sokolov et al., 2011](#)) at recognizing bodily emotions, such as identifying actions as happier, sadder, angrier or no different from a preceding neutral action. Specifically, females were more accurate than males in recognizing angry and neutral body language, while males were more accurate than females in reading happy body language ([Sokolov et al., 2011](#)). Interestingly, emotion recognition of body language is modulated by the sex of the target: males recognize expressions of happiness in female locomotion faster and more accurately, while females seem to be better and faster at recognizing angry locomotion of males, which, from an evolutionary perspective, is consistent with mating-related and threat-avoidance goals in males and females, respectively ([Krüger et al., 2013](#)). This finding also raises another important issue, that is, whether different natural selection pressures acted upon specific neural circuits to sustain abilities that confer reproductive advantages. The studies reported above, in fact, may suggest, although speculative, that sexual selection could have rendered males more sensitive to females' social positive signals in the context of courtship and sexual behavior. The capacity to detect positive emotions in females could allow males to detect female interest and potential mating opportunities. Recent work has shown that social cues, such as smile, can affect sexual preference and the transmission of sexual preferences in others ([Jones et al., 2007](#)). While females, by being more accurate in reading emotions through body language, could better rate the behavioral/emotional quality of the potential partner in terms of his paternal care capacity and sensitivity to the woman's and children's needs. Clearly more extensive work is required to understand the possible functions and evolutionary implications of the above described gender differences.

Although *emotional contagion* seems to contribute to emotion recognition ([Hatfield et al., 1993](#)), there are few studies investigating gender differences in emotion contagion. In one study, females, compared to males, reported greater susceptibility to contagion and displayed more overt signs of contagion in a semi-naturalistic setting, for both positive and negative emotions ([Doherty et al., 1995](#)). Similarly, when providing support for a troubled friend, females experience more emotion contagion than males ([Magen and Konasewich, 2011](#)). In fact, females report experiencing emotion contagion more often than males in their daily lives ([Kevrekidis et al., 2008](#)). Females, compared to males, exhibit greater facial mimicry when viewing expressions ([Dimberg and Lundquist, 1990](#); [Lundqvist, 1995](#); [Sonnby-Borgström et al., 2003](#)) and rely more than males on facial feedback for recognizing facial expressions ([Stel and van Knippenberg, 2008](#)).

Another approach to the study of emotional contagion examines pre-reflective emotional processing using an *emotional priming* method in which participants are exposed to negative or positive emotional cues outside of conscious awareness, such as happy or sad faces (Donges et al., 2012). In one study, participants were presented with a face prime expressing either happiness or sadness, followed by a neutral face, and then asked to evaluate how happy or how sad the neutral face appeared. They report that females tended to identify neutral faces as happier than males, and hence females, compared to males, were more affected by happy face priming (Klauer, 1997). This suggests that females might have a greater ability than males to perceive happy emotions at the pre-reflective level in visual stimuli (for similar findings in auditory stimuli: Schirmer et al., 2007). In another study, participants were primed to be in either happy or sad moods using short film scenes, followed by measures of participants' emotion recognition accuracy (Schmid et al., 2011). They report that males primed for a happy mood recognized facial emotions more accurately than when primed for a sad mood, while females did not show any significant priming. Additionally, eye tracking research revealed that females tended to process facial expressions more globally (i.e., attending to the whole face rather than localized areas) than males and were more accurate in emotion recognition. Furthermore, participants used more global processing after being primed for happy mood rather than for sad mood. However, only males became more accurate in recognizing emotions when primed for happiness. Together these results suggest that females seem to use global processing by default and therefore are not as affected by happy mood primes, while males do not use global processing by default and are therefore more sensitive to the happy prime. In related work, females fixated more on the eye regions of faces, compared to males, which may also be related to the female advantage in facial expression recognition (Hall et al., 2010), and which appears positively associated with empathetic skill (Cowan et al., 2014).

While generally it seems that females are either significantly faster or more accurate (or both) at emotion recognition, some studies show no gender differences (Klein and Hodges, 2001). This failure to find differences may be due to variation of experimental contexts and designs. For example, females were less accurate than males at judging interpersonal behavior by verbal and nonverbal cues if they thought that they were being tested on interrogation skills in the military (a historically masculine occupation), while males were less accurate if they thought the test measured judgment skills necessary for social workers (a historically feminine occupation) (Horgan and Smith, 2006). Higher empathic accuracy scores in females might be driven by motivation to appear more empathic (Klein and Hodges, 2001). They did not find any significant differences in empathic accuracy between males and females when they were asked to complete a sympathy questionnaire after the empathic accuracy test. However, females performed better if they had to fill in the questionnaire before the task. The results suggest that females are motivated to try harder to understand other people's feelings during the task if they think that what is measured is relevant to a stereotypical female role (sympathy). *Although motivational differences between males and females may account for some of the reported findings of female advantages in empathy, they cannot explain female advantages in automatic/unconscious nonverbal perception* (e.g., Donges et al., 2012), *or female advantages in populations that do not exhibit social desirability biases, such an nonhuman animals and infants, reviewed below.*

3.2. Mentalizing

Mentalizing is a largely conscious, deliberative process by which individuals take others' perspectives and infer others' intentions and beliefs (Zaki and Ochsner, 2012). As such, it is a major component of empathy. In contrast to findings on affective responsiveness and emotion recognition, there is inconsistent evidence for gender differences in ToM, or the ability to conceive of others' mental states, including what others' know, want, feel, or believe (Premack & Woodruff, 1978). While there are a number of studies in children that report female advantages in ToM, reviewed below, there are fewer studies in adults examining ToM, in general, as it is assumed that adults already have mature ToM abilities.

In a study on *visual perspective-taking* (a precursor to ToM), males, but also females with relatively high autism spectrum disorder (ASD)-characteristic personality traits were slower in perspective-taking than females with low ASD traits, suggesting that high-ASD-trait individuals, regardless of sex, may show lower fluidity in adopting another's visual perspective. This difference in visual perspective-taking hints at differences in the more general ability to understand what others see, think, and feel. Some sex differences in ToM tasks may be driven by the fact that males, compared to females, report that they less often adopt someone else's perspective during everyday situations (Pearson et al., 2013). Studies of imagined perspective transformation (in which the participant has to mentally adopt a different perspective from their current one, relative to an external object) suggest an increased emphasis on visuospatial processes in males during perspective-taking, rather than the social–emotional perspective-taking processes in which females typically show an advantage (Gardner et al., 2012; Meneghetti et al., 2012).

Only one study, to our knowledge, reported a male advantage in ToM (Russell et al., 2007). In this study, participants viewed 12 cartoons, half of which require an understanding of the cartoon character's mental state in order to "get" the joke, and half of which require an understanding of physical state to "get" the joke. Males outperformed females on both the mental and physical state cartoons. The authors concluded that this advantage was potentially due to a greater emphasis on cognitive-systematizing strategies in males.

These studies suggest that there may be gender differences in cognitive forms of empathy, such as perspective taking and ToM. These differences, however, may also be influenced by contextual factors (hence some apparently inconsistent findings). This contextual modulation may be key to a better and more nuanced understanding of gender differences in empathy based on the interaction between multiple processes. Indeed, there is evidence to suggest that cognitive and affective forms of empathy operate in an interactive way, with each contributing information and modulation to the other (Decety and Moriguchi, 2007; Chrisov-Moore and Iacoboni, under review).

3.3. Prosocial behavior

Since empathy aids in understanding others' emotions, it is also likely to be a major driving force in pro-social behavior. There has been a growing body of research investigating altruistic behavior (e.g., helping, sharing, volunteering) by means of economic games and self-report studies linking empathy to pro-sociality. As we review next, these studies indicate not only that the level of empathy is positively correlated with pro-social behavior, but also that females may be more empathic and thus more altruistic than males.

3.3.1. Economic behavior

One of the most common ways of investigating pro-social behavior in human adults is with economic games. In the *Ultimatum Game,* two individuals (a proposer and a responder) divide up a sum of money between them, based on the proposer's offer of a division of the total sum. The responder can then either accept (both get the money) or reject the offer (both get zero). It is important to note that offers are rejected mostly when considered to be unfair. One study found that females accept offers more frequently, and also that females' offers are accepted more often, although there were no sex differences in the amount offered (Eckel and Grossman, 2001). In contrast, another study reported the opposite: that female offers are rejected more often by both sexes, with the lowest acceptance frequency in female-female pairings, suggesting that females' expectations for a fair behavior is higher when facing another female (Solnick, 2001). This may explain why cooperation rates among females are lower than among males or among mixed-sex pairings (Balliet et al., 2011); it could be that females have higher expectations of other females and/or are more likely to try to take advantage of other females, compared to interactions with male partners. Additionally, participants had to identify the minimum offer they would still accept which revealed that the responders of both genders set their minimum acceptable offers higher when paired with female proposer. The inconsistency of the results in these two studies is likely due to different experimental conditions. In Eckel and Grossman (2001) the participants had face-to-face interactions while in Solnick (2001) they did not see each other, and greater strategic thinking might have been invoked when participants were asked to indicate their minimum acceptable offer. In a three-party Ultimatum Game, where a proposer had to divide the money between him/herself, a responder and a non-responding third player, females are more likely to offer an equal three-way split then males (Guth et al., 2007). This suggests that female behavior in economic games might in fact be altruistic rather than strategic. These findings indicate a higher level of altruistic behavior in females (Croson and Gneezy, 2009).

In the *Dictator Game* – a similar game to the Ultimatum Game except the recipient must always accept the offer – females give twice as much as males when the gender of receiver is anonymous, compared to when the gender is known (Eckel and Grossman, 1998). In another study, female participants, compared to male participants, gave less to females, while female participants' sharing with males or with individual of unknown gender did not differ, and male participants' behavior was not influenced by the target's gender (Ben-Ner et al., 2004). In a two-sided dictator game, a proposer divides the given sum of money between him/herself and a responder. The responder gets triple the amount of what the proposer offers and then has to divide that sum between him/herself and the proposer. Using this design with the players' genders unknown, females responders tended to return more money (i.e., act more prosocially) than males (Croson and Buchan, 1999). The self-report questionnaires filled in by the participants after the game indicated that females felt more obliged to return at least the same amount as they were given. This suggests that females' decisions in this particular experimental setting might be driven by reciprocity rather than altruistic behavior. Indeed, there were no significant gender differences in the amounts offered by the proposers. These results are inconsistent with those of Eckel and Grossman (1998) because they do not show greater altruistic behavior in females. In fact, experiments investigating how specific situational factors influence altruistic behavior showed that females appear more generous when the motivation for reciprocity is eliminated, e.g., during the dictator game where there is no interaction between the proposer and the responder. Furthermore, the social distance of the participant to the recipient, where knowing the name of the responder indicated low social distances, and not knowing indicated high social distances, could predict the level of generosity in females. This suggests that inconsistent findings across studies may be due to complex modulatory factors as well as due to greater female sensitivity to different experimental conditions

(Cox and Deck, 2006). Furthermore, Andreoni and Vesterlund (2001) performed a dictator game study in which participants had to allocate eight different budgets of money consisting of tokens of different values. Each budget had different relative prices of self-payoff and other-payoff meaning that, for some budgets, keeping value was higher than giving value and vice versa. The study revealed that females gave more than males when giving was expensive, which caused more fair sharing. Males gave more than females when giving was cheaper, ensuring higher payoff for themselves. These results suggest that males' sharing behavior is more sensitive to contextual factors than females' sharing behavior. In a nutshell, the presented collection of economic behavior studies suggests that females are more inequality-averse while males base their decisions on efficiency. *However, taken together, findings from the economic literature seem to indicate a higher level of altruistic behavior in females* (Croson and Gneezy, 2009).

3.3.2. Naturalistic data: Volunteering, donating, and other altruistic behavior One may argue that the results yielded by economic game studies do not necessarily apply to real life situations. In other words, they may have little ecological validity. However there are reports of charitable giving and hours of volunteering between males and females that do support the experimental findings. Empathic concern and helping behavior is positively correlated with generosity for both genders (Mesch et al., 2011). Females tend to score higher as well as donate more and more often (Mesch et al., 2011). Furthermore, females tend to volunteer more often and more hours than males (Mesch et al., 2006). In experimental studies, females are usually more likely to help than males (Eckel and Grossman, 2008). Females exhibit more caring prosocial moral judgment (Jaffee and Hyde, 2000) and exhibit more sophisticated forms of prosocial moral reasoning (Eisenberg et al., 2014). Females give more of their time and money to charities (for a review, see Einolf, 2011). Furthermore, in a study by Aguiar et al. (2009) participants were instructed to choose between male and female boxes containing slips of paper describing their intake from the dictator game (participants' payoffs depended on the amount written on the slips). 63% of the participants chose the female box and 79% of female participants chose the female box. This suggests that female participants are also expected to be more altruistic. However, in terms of amount donated per person, males give higher amounts than females (Piper and Schnepf, 2008); although, this may be due to higher incomes, on average, for males, or due to the fact that males are more likely to display their resources as a mating signal (e.g., Iredale et al., 2008).

While males help more often in certain contexts, females help more in other contexts. For example, females are more likely to help in *low-risk–low-physical-strength* (LRLS) situations, such as to look after neighbor's pet or give clothes to charity (Erdle et al., 1992). Males, on the other hand, tended to help more in *high-risk–high-physical-strength* (HRHS) situations (e.g. helping to push a car, giving a stranger a lift in a car). Both helping dimensions were positively correlated with outgoing personality characteristics and conventionality (value for responsibility and organization) in males. In contrast, HRHS was negatively correlated with conventionality, and LRLS was positively associated with open-mindedness in females. These results are consistent with both social roles (nurturing and caring by females vs. heroic defending and chivalry by males) as well as biological perspectives (greater physical strength and size of males). Social distance was also shown to have an effect on the tendency to help. A study using self-report questionnaires found that the likelihood of helping could be predicted by social closeness only in females, with females, but not males, being more likely to help a friend then a stranger (George et al., 1998). Moreover, male helping in general was more action-oriented (e.g., helping change a tire) while females seemed to be more likely to help with emotional concepts and provide sympathy.

Although it seems females are more altruistic, there are also sex differences in females' and males' reasoning/justification for helping (or not helping). While males and females tend to be prosocial when given hypothetical situations, their reasoning differed: Females' decisions seemed more empathy-related and they appeared happier about their decision compared to men, as indicated by self-report questionnaires (Mills et al., 1989). In addition, males' decisions on giving were more influenced by descriptive norms (beliefs of what most people do), which also indicated that men were more concentrated on self-presentation rather than exhibiting truly altruistic behavior (Croson et al., 2010).

In summary, studies of experimental economic games and the analysis of naturalistic data of charitable and volunteering behavior show that the majority of the data does reflect higher altruism in females.

4. Sex differences in the development of empathy in humans   Go to: ☑

4.1. Precursors to empathy in infancy: Emotion contagion, mimicry, and social interest

Rudimentary forms of empathy may exist in infants – perhaps facilitated by the matching and synchronization of emotional facial expression – behaviors that appear to promote emotional closeness of mothers and infants (e.g., Murray et al., 1996). The degree of emotional synchrony can be determined by monitoring mother–infant physiology (e.g., heart rate: Feldman et al., 2011), or behavior (de Waal, 1989; Sagi and Hoffman, 1976). For instance, *contagious crying* is a phenomenon in which human infants cry when they hear others cry (Martin and Clark, 1982; Sagi and Hoffman, 1976; Simner, 1971; Ungerer, 1990; Zahn-Waxler and Radke-Yarrow, 1982), but not when they hear other control sounds (Dondi et al., 1999; Martin and Clark, 1982; Sagi and Hoffman, 1976; Simner, 1971). Thus, infants' reactive crying is more than simply an arousal response to an aversive noise, but rather appears a specific response to emotional social stimuli, possibly reflecting emotional contagion.

Although we know of no studies that have examined sex differences in newborns' physiology in response to emotional social stimuli, a number of studies have examined sex differences in newborns' behavioral reactions. For example, from birth, there appear to be sex differences in social behaviors (for a review, see Alexander and Wilcox, 2012), including potential precursors of empathic predisposition (McClure, 2000). Female neonates, compared to males, are more likely to cry and cry longer when hearing another infant cry (Hoffman, 1977; Sagi and Hoffman, 1976; Simner, 1971). Female neonates, compared to males, also make more eye contact (Hittelman and Dickes, 1979) and are more likely to orient to faces (Connellan et al., 2000) and voices (Osofsky and O'Connell, 1977). This general social interest and responsiveness may reflect precursors or foundations of empathy because they provide infants with opportunities to learn about the behavior of other individuals. Infants who are less socially interested and/or attentive will not learn as much about other people. Some have proposed reduced social tuning may be a potential factor contributing to autism (i.e., Chevallier et al., 2012), a disorder characterized by impairments in social competence and empathy (Baron-Cohen et al., 2005). Specifically, typically developing infants – and female infants especially – prefer social stimuli, which preferentially capture their attention, and find social stimuli particularly rewarding, creating opportunities for social learning and to strengthen social bonds. Children that will eventually develop autism, in contrast, spontaneously

attend less to social stimuli, thereby limiting their exposure to critical opportunities for social learning (Chawarska et al., 2013). Thus, early differences in social motivation or social interest may account for some individual differences in social functioning later in life.

Human infants' sensitivity to facial expressions is important early in life, as it aids them in learning about their environment. For example, if an adult produces a fearful expression in response to a novel object, infants will modulate their response accordingly. As Darwin (1872) noted, "The movements of expression in the face and body, whatever their origin may have been, are in themselves of much importance for our welfare. They serve as the first means of communication between the mother and her infant; she smiles approval, and thus encourages her child on the right path, or frowns disapproval" (pp. 365–366). He also aptly observed "Every one must have noticed how readily children burst out crying if we pity them for some small hurt." (p. 218). Thus, children can use others' emotional reactions to assess their own situation and appropriate emotional reaction.

Newborns also imitate these facial expressions, including expressions of fear, sadness, and surprise, a phenomenon known as *neonatal imitation* (Field et al., 1982). Only one study to date has specifically examined sex differences in neonatal imitation, and found that female neonates, compared to males, were more skilled at imitating finger movements (Nagy et al., 2007). More studies of sex differences in infants seem necessary, given that the ability to spontaneously mimic facial expressions may be a skill underlying several social behaviors and competences, including empathy (e.g., Oberman et al., 2007; Sonnby-Borgström, 2002). Motor mimicry is one way through which children can learn about the experiences of others (McDonald and Messinger, 2011). Interestingly, typically developing children automatically mimic facial expressions, while children with autism do not appear to do so (Oberman et al., 2009). Disorders characterized by impaired empathy, including autism, are more common in males than females (Blair, 1995; Charman et al., 1997; Dodge, 1980; Baron-Cohen, 2002), and males also appear to be more susceptible to impairments in empathy. For example, one way in which male infants appear more susceptible to impairments in empathy is through their pacifier use. Specifically, infants' pacifier use – which decreases facial mimicry – predicts, and is negatively associated with, later perspective taking and emotional intelligence in males, but not in females (Niedenthal et al., 2012). In other words, males may be more negatively impacted by interference with their facial mimicry early in development, which impacts their later emotion understanding (Niedenthal et al., 2012).

With increasing age, infants demonstrate increased understanding of others' facial expressions. At 3 to 4 months, females may discriminate and understand expressions better than males (McClure, 2000) as suggested by the fact that they exhibit more distress than males in response to a maternal *still-face*, a paradigm in which, after a face-to-face social interaction with the mother, the mother assumes a neutral face and is unresponsive to the infant (e.g., Mayes and Carter, 1990). Such differential facial processing may be due to differences in visual attention to faces at this age, with females focusing more on internal facial features (e.g., eyes, mouth), compared to males, who shift their gaze more between internal and external features (outer contours) (Rennels and Cummings, 2013). These sex differences in social attention continue later during development. Around 12 months of age, female infants, but not male, prefer to view the biological motion of facial expressions to non-biological motion (Lutchmaya and Baron-Cohen, 2002), and when confronted with novel situations, females, but not males, are influenced by maternal facial and vocal signals of happiness or fear (Rosen et al., 1992). Interestingly, when mothers were instructed to direct fearful expressions at their infants, mothers' expressions were less intense when directed at female infants compared to

male infants, perhaps reflecting the mothers' awareness of their infants' sensitivity to such expressions (Rosen et al., 1992). These findings are consistent with other reports that by the end of the first year of life, female infants, compared to males, are more responsive to their mother's voice, initiate more maternal social interactions, and spend more time in close proximity to their mothers (Gunnar and Donahue, 1980; Wasserman and Lewis, 1985).

4.2. Toddlers and older children: Prosocial behavior and cognitive empathy

Rather than simply becoming personally distressed upon seeing another individual in distress, older children may better recognize and understand distress in others, although personal distress may be a precursor to recognizing and understanding distress in others (Batson and Shaw, 1991; Hoffman, 1975). One way of measuring this distinction is through assessing *prosocial behavior*. While 1 to 1.5-year-olds often respond to distressed others by exhibiting distress themselves, by 2 years of age, nearly all children demonstrate helping behaviors when others appear in distress (Radke-Yarrow and Zahn-Waxler, 1984; Zahn-Waxler and Radke-Yarrow, 1982) and sometimes imitate distressed behaviors of others (Zahn-Waxler et al., 1977), perhaps to try to understand such expressions (Thompson, 1987). By 1 to 2 years of age, female children in these situations show greater concern (e.g., sadness, sympathetic vocalizations, comforting) than male children (Hoffman, 1977; Volbrecht et al., 2007; Zahn-Waxler et al., 1992a). Similarly, a twin study of infants aged 14 to 20 months reported that females, compared to males, had higher empathy scores in their empathetic reactions to others' distress, and that empathy was moderately heritable (Zahn-Waxler et al., 1992b), consistent with another twin study in 14 to 36-month-olds (Knafo et al., 2008). This work is generally consistent with the notion that at least some aspects of empathy – including empathetic concern and personal distress – are moderately heritable (e.g., Chakrabarti and Baron-Cohen, 2013; Davis et al., 1994; Volbrecht et al., 2007), and in fact, it is estimated that approximately half of all variability in self-reported altruism may be due to genes (Rushton, 2004). In addition, it appears that the heritability of empathy may differ for males and females (e.g., Ragsdale and Foley, 2012; Lewis and Bates, 2011).

As children get older, their empathic predisposition acquires more cognitive layers, including what is often called *perspective taking*. In a study, 4- to 5-year-old children were shown videos to elicit personal distress, including videos of children frightened by a thunderstorm, saddened by the loss of a pet, or struggling to walk due to deformities (Eisenberg et al., 1988). Though there were no sex differences in heart rate, children did vary in their self-reported emotions (i.e., verbal reports and pointing to facial expressions), with females reporting more vicarious emotions. In another study, when 4-year-olds were shown photos of children in various emotion-evoking situations and were asked how they felt, females reported more empathetic emotions than males (Hoffman and Levine, 1976). A study of 5- to 13-year-old children's reactions to an infant crying found that females were better than males at both guessing causes of the infant's distress (indicating better perspective-taking) and thinking of ways to comfort the infant (Catherine and Schonert-Reichl, 2011). By 2 to 6 years of age, females outperform males in false belief tasks (Charman et al., 2002), a classical test of ToM. A study of preschool children's theory-of-mind understanding and social competence reported that, after controlling for age, theory-of-mind understanding significantly predicted aggressive or disruptive behavior for boys and prosocial behavior for girls (Walker, 2005). Theory-of-mind understanding also was related to lower scores of shyness or withdrawn behavior for boys. This may suggest that ToM is devoted toward differing goals in males and females, with males tending to seek dominance and females tending to seek conciliation (Walker, 2005).

In self-reports of empathy, females report higher levels than males from about 5 to 9 years of age (Chapman et al., 2006; Hughes et al., 2005). In this line of studies, experimenters often show photos or videos of individuals in varying emotional states and ask children to describe their own emotional response to the picture (e.g., Feshbach and Feshbach, 1969; Feshbach and Roe, 1968; Levine and Hoffman, 1975), to pick a corresponding emotion that matches a film (Hamilton, 1973), or to match a facial expression to an emotional picture, during which time children's expressions are rated (Buck, 1975). In one of these studies, second and fifth graders watched a video about individuals who had been in car accidents and were now in the hospital with injuries. The study shows that females exhibited more sad expressions and reported more sympathy and distress than males (Eisenberg et al., 1991), consistent with other studies in older children that found greater empathy in females than males (Feshbach and Feshbach, 1969; Feshbach and Roe, 1968; Levine and Hoffman, 1975). It must be noted that both male and female children appear more empathetic toward same-sex individuals (i.e., males more empathetic to males, and females more empathetic to females; Feshbach and Roe, 1968). In 10- to 13-year-old children, females appear to be better than males at understanding feelings and intentions of story characters (Bosacki and Wilde Astington, 1999), a finding that is consistent with similar findings in late adolescence (age 9 to 17 years; Hatcher et al., 1990). Female children, age 7 to 11 years, are also more likely than male children to recognize faux pas, such as when a speaker says something without a consideration of the listener (e.g., socially awkward or tactless), resulting in negative social consequences (Baron-Cohen et al., 1999). Compared to males, females, age 3 to 12 years, are more concerned about sharing, turn taking, and cooperating (Charlesworth and Dzur, 1987; Knight et al., 1989). By late childhood, females are better at identifying nonverbal emotional cues (Blanck et al., 1981; Hall, 1978).

Male children may have more control over their empathy or may not empathize as automatically as female children. For example, in 6- to 7-year-old children, male children show higher rates of donations to those in need when instructed to be empathetic (i.e., imagine themselves in the other person's situation), while females are equally empathetic whether instructed to do so or not (Brehm et al., 1984). Such effects may be similar to findings in adults that males, but not females, are less empathetic toward social partners who are perceived as behaving unfairly (Singer et al., 2006). In this way, males may be more sensitive to contextual influences on their empathy and their empathy may be more dependent on their motivational state (Ickes et al., 2000).

As mentioned previously, facial mimicry seems associated with empathic predisposition (e.g., Oberman et al., 2007; Sonnby-Borgström, 2002). In 6 to 7 year-old children, individuals with autism who score lower on social responsiveness also are less likely to mimic fearful expressions, as measured by facial electromyography (Deschamps et al., 2013). Contagious yawning may also be associated with empathy (Preston and De Waal, 2002). This behavior does not appear until around 5 years of age (Anderson and Meno, 2003). While there are no studies that specifically examined whether there were sex differences in contagious yawning throughout childhood, when contagious yawning was compared between 7 to 15 year old children, with and without autism, only typically developing children displayed the behavior (Senju et al., 2007). When children with autism were instructed to focus their attention on the eyes, however, they were just as likely to contagiously yawn as typically developing children (Senju et al., 2009), consistent with the proposal that atypical social orienting may negatively impact empathy in autism (Chevallier et al., 2012).

4.3. Empathy in adolescence

Females are more prosocial, sympathetic, and empathetic than males, from childhood through adolescence (for reviews, see Chaplin and Aldao, 2013; Rose and Rudolph, 2006). The transition into adolescence appears to widen the differences in empathy between males and females (e.g., Lam et al., 2012). In one study, high school students completed four empathy questionnaires, and while overall there were improvements in empathy with age, females scored higher than males on all measures (Davis and Franzoi, 1991), a finding that is consistent with previous studies of empathy in adolescents (e.g., Adams et al., 1979; Auyeung et al., 2012; Davis, 1980; Feshbach, 1982; Hawk et al., 2013; Mehrabian and Epstein, 1972; Mestre et al., 2009). Adolescent females scored significantly higher in empathy and appeared to help victims being bullied more in comparison to males (Jolliffe and Farrington, 2006). Female adolescents also outperform males on tests of ToM (Ibanez et al., 2013). Interestingly, in adolescence, it appears that the sex of the individual in the stimulus modulates empathy in males but not females (Bryant, 1982; Olweus and Endresen, 1998). Specifically, in students aged 13 to 16 years, females showed developmental increases in empathy toward both males and females, while males showed, with age, increases in empathy to females, but decreases in empathy to males (Olweus and Endresen, 1998). Similarly, another study found that in 7th graders, but not in 1st or 4th graders, males exhibited greater empathy for females than for males, but females exhibited equal levels of empathy for both sexes (Bryant, 1982). These differences in empathy as a function of target sex have been interpreted in terms of different evolutionary selective pressures on males and females, especially with regard to issues associated with mating (Olweus and Endresen, 1998).

4.4. Summary and conclusions regarding sex differences in empathy across development

Together, this work suggests that there may be sex differences in emotional attunement and empathy beginning early in ontogenetic development. From this body of developmental work, it is clear that there are sex differences in empathy from birth, and sex differences appear to be consistent and stable across the lifespan (e.g., Michalska et al., 2013; O'Brien et al., 2013), with females demonstrating higher levels of empathy than males, and children who are higher in empathy early in development continue to be higher in empathy later in development (Eisenberg et al., 1999). This developmental stability suggests that sex differences are unlikely to be caused exclusively by postnatal experiences (e.g., maternal care), but rather reflect some evolutionarily important difference between males and females that is present, at least in some form, from birth, consistent with reports that empathy is moderately heritable (e.g., Baron-Cohen, 2002; Chakrabarti and Baron-Cohen, 2013; Knafo et al., 2008; Rushton, 2004; Zahn-Waxler et al., 1992a,b; Zahn-Waxler et al., 2001). Darwin was likewise interested in the extent to which sympathetic reactions were learned or present prior to experiences. He reported anecdotally about his son:

> I attended to this point in my first-born infant, who could not have learnt anything by associating with other children, and I was convinced that he understood a smile and received pleasure from seeing one, answering it by another, at much too early an age to have learnt anything by experience. When this child was about four months old, I made in his presence many odd noises and strange grimaces, and tried to look savage; but the noises, if not too loud, as well as the grimaces, were all taken as good jokes; and I attributed this at the time to their being preceded or accompanied by smiles. When five months old, he seemed to understand a compassionate expression and tone of voice. When a few days over six months old, his nurse pretended to cry, and I saw that his face

instantly assumed a melancholy expression, with the corners of the mouth strongly depressed; now this child could rarely have seen any other child crying, and never a grown-up person crying, and I should doubt whether at so early an age he could have reasoned on the subject. Therefore it seems to me that an innate feeling must have told him that the pretended crying of his nurse expressed grief; and this through the instinct of sympathy excited grief in him. (Darwin, 1872; pp. 359–360).

Sex differences appear to grow larger with age, especially around puberty, perhaps driven by greater age-related improvements in empathy in females relative to males (e.g., Eisenberg et al., 1989; Michalska et al., 2013; Van Tilburg et al., 2002). However, the use of different (age-appropriate) measures at different ages may account for some of these apparent age-related changes in the degree of sex differences. In other words, measures used at later ages in development (e.g., adolescence) may be more sensitive for detecting sex differences than measures used earlier in development (e.g., infancy).

A number of studies emphasize the role of social influences on empathy, proposing that parents can support empathy in their children, either as role models or through fostering healthy, secure attachments (e.g., Barnett et al., 1980; Eisenberg and Valiente, 2002; Knafo and Plomin, 2006; Koestner et al., 1990; Mehrabian et al., 1988; Miklikowska et al., 2011; Strayer and Roberts, 2004). However, these differences could also be due to genetic predispositions shared between parents and children, as some data suggest that empathy may be heritable, as already mentioned. It is also possible, however, that *social motivation – which appears to differ between the sexes – may be a driving force behind developmental sex differences in social skills, such as empathy* (e.g., Chevallier et al., 2012). Early differences in social attention between male and female infants seem to occur prior to socialization, appearing even in newborns (Alexander and Wilcox, 2012) and thus probably contributing to females' greater sensitivity to others' emotions, compared to males.

Finally, though it has been explored little, it appears that the type of stimulus (e.g., sex of stimulus) has an important impact on male but not female empathy (Bryant, 1982; Olweus and Endresen, 1998). Although speculative, it is possible that this differential responding as a function of target sex may account for some of the sex differences reported across development. Specifically, it may be the case that males are not necessarily less empathetic than females, but that they direct varying levels of empathy at different types of social partners, with female targets eliciting equal levels of empathy from male and female viewers and male targets eliciting greater empathy in female viewers compared to male viewers. Of course, this would still render males, on average, less empathetic than females. In addition, males have more deliberate control over their production of expressions, and this control increases with age (e.g., Eisenberg et al., 1989), so many of these measures that rely on overt signals of empathy may find lower levels in males than females. *Given that males have more control over their emotional expressions, they may likewise have more control over their empathy* (Brehm et al., 1984). Though this hypothesis has not been directly tested in healthy populations – to our knowledge – it is consistent with data demonstrating associations between various disorders and empathetic control. For example, studies report a positive association between control of empathy and depression (Thoma et al., 2011), a disorder significantly more common in females than males (Weissman et al., 1996), while psychopathy and autism – disorders both associated with less spontaneous empathy (Gillespie et al., 2014; Senju et al., 2009) – are more common in males than females (Baron-Cohen et al., 2005; Cale and Lilienfeld, 2002). In fact, in both psychopathy and autism, though individuals may exhibit less automatic

empathy, when explicitly instructed to be empathetic (i.e., under effortful control), they are capable of exhibiting significantly higher levels of empathy (Gillespie et al., 2014; Meffert et al., 2013; Senju et al., 2009; related, spontaneous vs. deliberate mimicry in autism: McIntosh et al., 2006; Oberman et al., 2009). Together, these studies suggest that sex differences in empathetic control may play a role in various disorders associated with abnormally high or low levels of empathy, and that the distinction between empathy ability and propensity is particularly relevant for examining individual differences (Keysers and Gazzola, 2014; Keysers et al., 2014).

Nonetheless, a developmental perspective can provide insights about the proximate and ultimate causes of individual differences in empathy. Based on the evidence summarized here, it is difficult to deny that there are differences in empathy between males and females. The evolutionary and proximate causes of these differences, however, remain largely unexamined, and are, we think, an important future direction for this work.
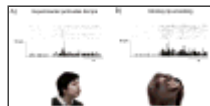
5. Neuronal mechanisms for empathy

5.1. Mirror neurons

In emphasizing that empathy is a multilayered phenomenon, several scholars converge in considering an action–perception mechanism as central for automatically reproducing others' affective states (Preston and De Waal, 2002; Iacoboni, 2009). Much theoretical discussion has been stimulated by the discovery of *mirror neurons* in the ventral premotor cortex and the inferior parietal lobule of the monkey (Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996). These neurons have the peculiar feature of firing both when a specific action is observed and when another individual performs the same action. In the original work, and in most studies that have followed, monkeys were trained to perform or observe a goal-directed hand action. The most important property of mirror neurons is the congruence they show in their responsivity between the effective observed and the effective executed action (Rizzolatti and Craighero, 2004). This property, together with the fact that mirror neurons have been found in cortical areas involved in motor control (Keysers and Fadiga, 2008), has led to the proposal that others' actions can be translated into a motor code exploiting one's own action knowledge, in terms of an individual's cortical motor representations (Iacoboni et al., 2005). This translation allows an observer to map others' actions onto the internal motor representation of that action, allowing the observer to understand the observed actions.

This mechanism became even more significant for empathy research when subsequent findings showed that mirror neurons consisted of not only visuomotor neurons discharging for hand actions, but also that some made up a class of neurons specifically driven by actions performed with the mouth (Ferrari et al., 2003). Crucial to the involvement of mirror neurons in empathy, a percentage of mirror neurons were revealed to respond while the monkey observed affiliative communicative gestures (i.e., lips-macking) (Fig. 5).

Fig. 5
An example of mirror neuron (Unit 76) activating during the observation of an affiliative facial gesture, typical of macaques, made by the experimenter (left) and during the observation of a

similar gesture performed by the monkey (right) (from [Ferrari] **...**

These were the first single-unit data recorded from the classical mirror neuron system that strongly suggest that the postulated mechanism by which a mapping of the observed action onto an internal motor representation could be reasonably extended into the emotional domain.

Another interesting aspect of mirror neurons in relation to empathy is that some mirror neurons show a *multimodal nature*. In fact, a study found that some of them fire not only during the observation of action, but also while listening to the sound of that action, alone ([Kohler et al., 2002]). The responses of these neurons were specific for the type of action seen and heard. For example, they responded to peanut breaking when the action was only observed, only heard, or both heard and observed, and did not respond to the vision and sound of another action, or to non-action sounds (e.g., environmental noise). Neurons responding selectively to specific action sounds were named "audio-visual" mirror neurons ([Kohler et al., 2002]). This finding exemplifies the idea that the matching can be generated not only through a mapping of a single sensory modality with the motor representation of the action, but that the matching can be multimodal. During empathic experiences, in fact, subjects can activate shared motor representations by exploiting multiple sensory channels, including visual, tactile, and auditory channels.

Despite these early studies, no other work explored the issue of mirror neurons and empathy through *single cell recording*. This leaves open a number of interesting questions, such as the extent to which there are individual differences – including sex differences – in the activity of mirror neurons, and whether such differences, if they exist, might be associated with empathetic skills. Animal models of autism, combined with single cell recordings, might be insightful for disentangling differences in the brains' response to social stimuli, as well as for assessing potential therapies.

In humans, single cell recordings have demonstrated that a mirror mechanism is present and, despite limited evidence, findings are supportive of the proposal of a basic action–perception mechanism involvement in empathy ([Hutchison et al., 1999]; [Mukamel et al., 2010]). In one study on patients undergoing surgical procedures for psychiatric treatment, there were anecdotal observations of a few neurons in anterior cingulate cortex responding not only while they received painful stimulation but also when the patient watched the surgeon apply a painful stimulation to himself ([Hutchison et al., 1999]). A more extended study with depth electrode recordings in human mirror neurons investigated 21 patients undergoing surgery for otherwise intractable epilepsy ([Mukamel et al., 2010]). The patients, in addition to executing and observing grasping actions, also performed two facial expressions (smiling and frowning) and observed the same facial expressions. Mirror neurons were observed in the SMA, hippocampus, parahippocampal gyrus, and enthorinal cortex. Among the 68 units with mirroring properties, 14 had opposite firing rate changes. The majority of these cells had increased firing rate for action execution, and decreased firing rate for action observation.

Together, these findings support the proposal that, during the observation of facial expressions, mirror neurons in several areas are recruited and might support basic forms of facial mimicry or emotional contagion, so well described at the behavioral level. Clearly these types of rare and invasive investigations are not suitable for exploring the possible gender differences related to these basic forms of brain mirroring.

Therefore, in the next sections we will review how the principles of brain mirroring are explored by means of other, more feasible, neuroscience methods and whether the brain responses during perception and expression of facial expression differ in males and females.

5.2. Neural human gender differences: Foundational issues, tools, and methods

It is especially important to better understand gender differences in neural systems relevant to empathy. Indeed, there is general consensus that empathy is a cornerstone of social cognition and that social cognition is a key component of mental health. Since the prevalence, age of onset, and symptomatology of many psychiatric conditions differ between males and females (for instance autism, attention deficit/hyperactivity disorder, antisocial personality disorder are more common in males whereas depression, anxiety disorder, and anorexia nervosa are more common in females), a better understanding of empathy-related gender-differences in neural organization may provides clues to unravel the neurobiological bases of these disorders.

As we have already seen, at cellular level we know of a mechanism – mirror neurons – that is a strong candidate for being associated with empathy. Obviously, mirror neurons cannot be the only cellular elements that enable empathy. Yet, of all cellular mechanisms already discovered by neurophysiological investigations, mirroring seems the easiest and most natural one to be associated with empathy, given its functional properties. In humans, however, single cell recordings can only be performed under extremely unusual circumstances. These circumstances, as stated before, typically preclude the study of gender differences, due to the small number of patients investigated. Hence, the study of mirroring in humans is typically performed in an indirect, non-invasive way by using Transcranial Magnetic Stimulation (TMS), electroencephalograhy (EEG), magnetoencephalography (MEG), and functional magnetic resonance imaging (fMRI). These techniques can also be used to study the neural correlates of empathy and its gender differences, both in mirroring systems and in neural systems that have little or nothing to do with mirror neurons (i.e., mentalizing systems), but which may also support empathetic abilities. We discuss each of these techniques, first addressing the studies inspired by mirror neuron research, and then studies encompassing other systems in the brain.

5.2.1. TMS: Cortico-spinal facilitation The first human TMS study that was associated with the firing of mirror neurons used TMS to measure levels of cortico-spinal excitability of the motor system (Fadiga et al., 1995). The logic behind this kind of study is as follows. The premotor cortex contains mirror neurons that fire during action observation. The firing in premotor cortex should make the primary motor cortex more excitable. Hence TMS of the corticospinal motor system should reveal this increased excitability. Indeed, other studies reported larger *motor evoked potentials* (MEPs, that is, muscle twitch evoked by the stimulation of the motor cortex) when participants' motor cortex is stimulated during action perception, compared to control conditions (Aziz-Zadeh et al., 2002, 2004) and that they correlate with self-reported empathy, especially when the observed action has emotional significance (Avenanti et al., 2005). Thus, these data suggest that the TMS-measured motor corticospinal facilitation during action observation seems a viable marker of empathic predisposition. Notably, studies on gender differences in TMS-measured motor corticospinal facilitation are lacking. It is possible that such striking absence is related to the sample size of the studies. Indeed, these TMS studies tend to enroll fairly small sample sizes, which make it difficult to properly investigate gender differences.

In principle, however, TMS-measured corticospinal facilitation should reveal gender differences, if behavioral studies tend to show, on average, higher self-reported empathy in females. One measure that has more commonly been employed to study sex differences in empathy is *facial electromyographic* (EMG), which measures facial mimicry, and is positively associated with empathy (Dimberg et al., 2011; Dimberg and Thunberg, 2012) and facial expression recognition (e.g., Sato et al., 2013). Indeed, a number of studies report greater facial muscle reactivity in females, compared to males, when exposed to facial expressions (Dimberg and Lundquist, 1990; Lundqvist, 1995). Facial EMG activity was measured from the corrugator and zygomatic muscles, typically activated during angry and happy facial expressions, respectively. This muscle reactivity can be considered as a form of motor resonance, likely the expression of mirroring mechanisms that also produce the TMS effects described above. In this particular study, female subjects demonstrated higher EMG activity, compared to male subjects, thus supporting the idea that pre-reflective processes that may be foundational for empathy are more enhanced in females. Similarly, individuals with higher levels of autistic traits show less automatic facial mimicry, as measured by EMG (e.g., Sims et al., 2012).

5.2.2. TMS 'virtual lesion' studies Another way of using TMS to study neural systems in humans and their relations with behavior is the so-called 'virtual lesion' methods. Repetitive stimulation of a brain area interferes with its activity. When such stimulation results in a behavioral change, it is assumed that the functions of the stimulated area are somewhat associated with the behavior that was modified, (see for instance Heiser et al., 2003). There is a vast literature on this type of study. The power of these studies is that they make explicit brain–behavior relationships, revealing the causal role of a given brain region to a given behavior.

Indeed, a study combining the 'virtual lesion' method over the ventral premotor cortex, and the TMS motor cortico-spinal facilitation approach, described in the section above, recently provided evidence in support of the main idea behind TMS studies, that the activation of premotor mirror neurons makes the motor cortex more excitable. The interference of premotor activity with the TMS 'virtual lesion' method should abolish the expected increased motor excitability during action observation. Confirming the validity of the basic assumption behind TMS motor excitability studies of mirroring, repetitive TMS over the ventral premotor cortex abolished motor facilitation during action observation (Avenanti et al., 2007).

TMS 'virtual lesion' studies, especially when combined with economic games testing explicit prosociality (see previous behavioral section) are powerful experimental approaches to examine the role of neural systems in modulating empathy and prosocial behavior. In one such study, participants stimulated over the right dorsolateral prefrontal cortex (DLPFC) demonstrated a higher willingness to accept unfair offers from other players (Knoch et al., 2006). Typically, in these games, unfair offers (generally offers of less than 25% of the available money to be shared) are rejected, even though rejecting them means renouncing the monetary gain (but at the same time precluding the unfair offerer from making an unfair gain). This is considered evidence that humans tend to modulate self-interest with social norms and moral values such as reciprocal fairness, being willing to punish unfair behavior even if it means hurting self-interest. In this study, stimulation of the left DLPFC did not change the low acceptance rate of unfair offers, suggesting a striking laterality difference in the DLPFC with regard to reciprocal fairness. The behavioral change brought about by TMS has been interpreted as 'increased selfishness', that is, higher willingness to accept unfair offers in order to make a monetary gain. This interpretation rests on the fact that when asked whether offers sharing less

than 25% of the available money were fair or unfair, participants still considered them unfair, even though they were more willing to accept them. However, participants were asked about the perceived fairness of the offer only after the economic game was played, leaving open the possibility that the effects of TMS over brain activity were reduced during this part of the experiment (TMS effects are obviously only transient, not everlasting). An alternative interpretation regarding the higher willingness to accept typically considered unfair offers is that transiently interfering with the right DLPFC may have increased mirroring and perspective taking and potentially compassion, thus making it more likely to see things from the other player's point of view. In this view, increased acceptance of low offers is not due to increased selfishness but to increased empathy.

Regrettably, this experimental approach has not yet been used for larger scale studies that would allow tests of sex differences. A study of this sort would require a much larger sample size than is typically used in this literature. Given that TMS reveals causal relationships between brain activity and behavior, it is surprising that there are no TMS studies of empathy to date examining gender differences. Indeed, this may prove a fruitful avenue for future research in this field.

5.2.3. Magnetoencephalography (MEG) and electroencephalography (EEG): Beta rebound and mu suppression Both MEG and EEG demonstrate in central, sensory–motor regions oscillatory activity in the 10–20 Hz range at rest that desynchronizes during action performance and observation. The oscillatory activity resumes when participants go back to a 'resting state.' This pattern of neural activity is interpreted as representing another marker of mirroring at the level of neuronal ensembles, because desynchronization during both action execution and action observation is typically framed in terms of 'motor activation' (Hari et al., 1998). In the mirroring literature, two parameters have been used to quantify these changes in MEG and EEG signal in central sensory–motor regions: the beta rebound around 20 Hz (Hari et al., 1998) and the mu rhythm suppression around 9–13 Hz (Muthukumaraswamy and Johnson, 2004). The latter parameter has been also correlated with empathic predisposition (Cheng et al., 2008a,b). Two groups have reported increased mu suppression in female subjects, compared to males, thus supporting the hypothesis of higher mirroring and potentially empathy in females (Cheng et al., 2008a; Yang et al., 2009).

5.2.4. Event related potentials (ERP) studies of gender differences in empathy Gender differences in empathy using *event-related potentials* (ERP) have been demonstrated in a handful of studies. A study looking at an early, frontal waveform and a late, parietal waveform associated with pain perception demonstrated two kinds of gender differences: the early waveform was correlated with self-reports of perceived pain in females only, and the late component was more easily modulated by concurrent attentional task demands in females too (Han et al., 2008).

Two ERP studies investigated both the emotional valence (e.g., suffering vs. happiness) and the presence or absence of humans in pictures (Groen et al., 2013; Proverbio et al., 2009). Taken together, the results show increased amplitudes of ERP waveforms to humans suffering in females. The only study (Groen et al., 2013) that measured also self-reported empathy, however, found similar levels of correlation between neural activity and affective empathy in males and females.

In a rather unusual take on the investigation of gender differences in empathy, a recent study looked at the role of social context in language processing (van den Brink et al., 2012). Females demonstrated a larger N400 compared to males in such situations. Notably, the N400 also correlated with self-reported empathy in this study, thus suggesting that different degrees of empathy also affect the processing of linguistic information in social contexts.

A number of studies, however, report sex differences in ERPs during emotion processing, including emotion in the voice (e.g., Schirmer et al., 2007) and in the face (e.g., Xu et al., 2013), suggesting that females may be more sensitive to emotional signals. For example, females process emotion in the voice more automatically than males (Schirmer and Kotz, 2003).

5.2.5. Activation studies using functional MRI (fMRI) and mirroring markers The most common non-invasive technique to study functional brain responses in human living subjects is *fMRI*, because it allows full brain coverage and good spatial and temporal resolution. Indeed, a recent meta-analysis includes more than a hundred fMRI studies (Caspers et al., 2010) and supports the early conclusions that there are human brain hubs showing strong patterns of activity suggesting mirroring, including the posterior inferior frontal and the anterior inferior parietal cortex (Iacoboni et al., 1999; Iacoboni, 2005; Iacoboni and Dapretto, 2006).

An early fMRI study proposed that empathy is made possible through the interactions between mirror neuron areas and emotional brain centers (Carr et al., 2003). More recent fMRI studies focusing on gender differences in empathy seem to confirm this general idea. Indeed, a recent fMRI study on empathy has revealed gender differences in the inferior frontal cortex, suggesting that these gender differences may be due to differences in the mirror neuron system (Schulte-Rüther et al., 2008). Subjects were asked to focus on either their own feelings when seeing facial emotional expressions or the feelings of the other person. In both the 'self' and 'other' oriented attentional focus, females activated more the inferior frontal cortex, compared to males.

5.2.6. Gender differences in fMRI studies of empathy not related to mirroring In a study on the modulatory role of social reputation in pain perception, subjects first played an economic game with cooperative and non-cooperative confederates and then watched the confederates inflicted with pain (Singer et al., 2006). When watching someone in pain, a typical brain response is to activate a set of neural systems associated with experiencing pain. This mirroring vicarious activation is generally interpreted as a form of empathy, a kind of "I feel what you feel" automatic reaction. This mirroring response, however, is not entirely automatic; it can be modulated. Indeed, in this study on social reputation in pain perception, while both males and females demonstrated similar activation of pain-associated neural systems while watching cooperative players, males had reduced activation of pain-associated neural systems while watching non-cooperative players inflicted with pain. This reduced empathic response was also associated in males with activation of reward-related structures while watching non-cooperative players in pain. These rather striking gender differences suggest again that males are much more sensitive than females to contextual modulation of empathic brain responses. This study also suggests that mirroring responses during observation of others' emotions do interact with those brain structures that are involved in cognitive empathy.

5.2.7. Structural MRI A handful of studies have reported empathy-related gender differences in brain structures (Cheng et al., 2009). Females have larger grey matter volumes in both posterior inferior frontal and anterior inferior parietal cortex, two areas typically associated

with mirroring in the fMRI literature. Furthermore, empathic predisposition in females correlated with grey matter volume in the inferior frontal cortex, providing additional evidence in favor of gender differences in mirroring.

Studies on structural connectivity demonstrated correlations between white matter tracts and empathic predisposition in anatomical connections between mirror neuron areas and emotional brain centers (Takeuchi et al., 2013), supporting the findings from fMRI on the role of this large scale network including both mirror neuron areas and emotional brain centers in empathy.

5.3. Hormones, sexual preferences and gender roles

Prior to the introduction of neural measures of emotional responsiveness, it was unclear how much sex differences in empathy were simply due to differing gender stereotypes and strategies. In a 1983 review by Eisenberg and Lennon, they examined males and females' empathic abilities and found mixed evidence for inherent sex differences. Indeed, sex differences were found to vary dramatically when taking into account the manner of reporting empathy and the circumstances under which this was done. Sex differences in empathy favoring females were most evident when individuals were asked to *rate themselves* on empathetic behaviors and affective responses, while weaker differences were found when subjects were simply asked to rate their emotional responses in hypothetical scenarios. In contrast, sex differences were inconsistent when empathy was assessed with physiological measures (primarily skin conductance and heart rate) and/or facial/vocal/gestural measures (the latter of which only included studies of children). Indeed, there is evidence to suggest that males and females may differ in how empathetic they would like to *appear*, given that emotional responsiveness and nurturing behavior are part of stereotypical feminine roles. For example, sex differences in responsiveness to the young (a stereotypically feminine behavior) have been found in several studies, but only in situations in which it is clear that subjects are being evaluated on that dimension, or that role expectations or obligations are salient. Self-ratings of adults' femininity have been positively related to males' and females' self-report of empathy, whereas self-reported of masculinity has been negatively associated with empathy scores (Eisenberg and Lennon, 1983).

Indeed, while biological gender is clearly important, sexual preferences (e.g., Perry et al., 2013; Sergeant et al., 2006), within-gender differences in prenatal hormone exposure (e.g., Chapman et al., 2006), hormone reactivity, and, in females, effects of ovulatory hormones (Derntl et al., 2013) are highly important, suggesting that the complexity of defining gender is reflected in individual differences in empathy. Individuals sexually attracted to males showed greater empathy (in behavioral measures) and greater activation during an emotional judgment task in an area whose activation was correlated with self-reported empathizing, than subjects attracted to females (Perry et al., 2013). According to the *Empathizing-Systemizing Theory*, individuals vary on two factors –empathizing (ability to understand others' emotions and thoughts) and systemizing (ability to analyze or construct systems) – that can help us understand sex differences (Baron-Cohen, 2002). A study of empathizing and systemizing tendencies found that males and non-heterosexual females showed higher systemizing tendencies than heterosexual females, further suggesting that both biological gender and sexual preferences underlie differences in empathy (Nettle, 2007).

Fetal testosterone has been suggested to be one of the major factors determining sex-differences of empathy (Chapman et al., 2006). Testosterone decreases the ability to empathize (van Honk et al., 2011). Fetal testosterone levels in males and females were predictive of

their tendency to use intentional or neutral statements when describing characters in cartoons, suggesting that testosterone exposure can modulate the ratio between empathizing and systematizing traits (Knickmeyer et al., 2006). Variability among healthy children in their prenatal hormone exposure is related to individual variability in postnatal behavior. As in studies of atypical exposure, higher levels of androgen predict more male-typical, and less female-typical, behavior. A study of females' moral judgments found that changes in utilitarian judgments following exposure to testosterone were dependent on second-to-fourth digit ratio (a marker of prenatal androgen exposure) (Montoya et al., 2013). Hormone-induced alterations in brain development are thought to underlie these behavioral outcomes, although there is little information on specific neural differences associated with early hormone differences (Hines, 2008).

Another important field of research, which is becoming increasingly popular is the potential role of the neuromodulator *oxytocin* (OT), an endogenous neuropeptide associated with bonding and nurturing behavior. Following intranasal administration of oxytocin (OT), the serum level of OT is positively correlated with empathetic ability and generosity (Domes et al., 2007). A study of OT and *vasopressin* (AVP) administration's effect on prisoner's dilemma behavior with human and computer partners, both OT and AVP caused females to treat computer partners more like humans, and AVP increased their conciliatory behavior. In men, AVP selectively increased reciprocation of cooperation from both human and computer partners. No common drug effects on behavior were found in both males and females, though both OT and AVP increased activity in males in areas known to be rich in OT and AVP receptors, and in areas important for reward, arousal, memory and social bonding. Importantly, both OT and AVP increased activity in males during cooperation, while in females, OT and AVP either decreased activity or had no effect in these and other regions (Rilling et al., 2014). These results suggest that, as with androgens, while somewhat similar behavioral effects are observed, the neural processes for reacting to these substances may differ between males and females, resulting in distinct dose–response curves between genders. Indeed, another OT administration study found that OT exerted a greater effect on perspective taking in men. This study also found that self-report measures might be less sensitive to OT effects than more implicit measures of empathy. If these assumptions are confirmed, one could infer that OT effects on empathic responses are more pronounced in males than females, and that any such effect is best studied using more implicit measures of empathy rather than explicit self-report measures (Theodoridou et al., 2013).

The implication of these studies is that in assessing differences in such a complex construct as gender, researchers should take into account gender roles, circumstances of data collection, sexual preference, prenatal androgen exposure and hormone reactivity.

6. Conclusions   Go to: ☑

The construct of empathy is relevant to several disciplines, from psychology and neuroscience, to behavioral economics and animal behavior. For years, theories on altruism and kin selection have emphasized the selfish nature of humans and other animals. However, the 'selfish gene' paradigm faced serious challenges to the idea that individuals are complex organisms whose activities ultimately function to increase reproductive success, and do so through careful calculations of costs and benefits. Work on primates and other animals has shown that individuals prefer to act prosocially and in cooperation, they need to repair relationships after conflicts, support each other when in

need, and ask for comfort because they know that companions are sensitive to their own pain and suffering. Interestingly, most of these examples do not necessarily imply genetic relatedness or reciprocal benefits.

So what drives this empathetic nature? We propose that an examination of interindividual differences in empathetic skill –and sex/gender differences, specifically – can be informative for understanding the nature of empathy, including its proximate and ultimate causes. To this end, the present review had two primary goals: (1) determine whether sex/gender differences in empathy may be largely driven by cultural rather than biological causes through studies of younger populations and nonhuman animals, and (2) extend our understanding of the phenomenon of empathy itself—specifically, whether emotional and cognitive components are independent or related through neuroimaging and behaviors studies of gender differences in adult humans.

Empathy, at its core, is an ancient biological phenomenon and, according to one hypothesis, the roots of empathy can be found in the practice of caregiving, particularly in altricial species, whose offspring depend on the mother for a prolonged postnatal period (Preston and De Waal, 2002). Parents tune their behavior with that of their immature offspring. Such sensitivity is not only confined within the mother–infant relationship, but it includes other group members. In primates, living in large groups, such as in macaques or in chimpanzees, families or other social units are formed through relationships that can last the entire lifespan. Such complex social networks are sustained and maintained by the capacity of each individual to respond to the emotional signals of companions in various contexts, including situations of danger or discomfort, as well as during play and excitement. In primates, these phenomena are strikingly more evident if one looks at the complex and sophisticated anatomy of facial muscles, which primarily function to express emotions and to support emotional communication. Psychologically and cognitively demanding processes have shaped the mind of our ancestors, resulting in human social behaviors and empathic sensitivities to the internal state of others.

Indeed, in nonhuman animals, including primates and rodents, sex differences have been reported for a diverse number of behaviors believed to be indicative of empathy, including emotional contagion, facial mimicry, contagious yawning, sensitivity to conspecific's pain/distress, consolation, and prosocial behavior. Together, reports of these behaviors in nonhuman animals make a convincing case that females possess greater levels of empathy compared to males, in at least some species. If such sex differences were purely cultural in cause, then this implies that either animals are likewise transmitting cultural expectations of gender (possible, but unlikely), or, more parsimoniously, that such sex differences in humans are driven by some biological root, which humans share with other animals.

Furthermore, studies of human infants report evidence that females exhibit higher rates than males in various rudimentary forms of empathy, such as contagious crying, neonatal imitation, social referencing (i.e., looking to social partners for information in ambiguous situations), and general social interest and sensitivity. These studies allow us to rule out response biases (e.g., social desirability bias) as the sole cause of sex differences in humans, as well as allowing us to examine individual differences prior to much socialization, therefore ruling out cultural influences as the primary cause of sex differences, at least in young infants. With age, the pattern of sex differences remains stable, or, if anything, it appears to grow larger with age, potentially due to increases in empathetic skill, the increased sensitivity of empathetic measures that can be used in older children, or through actually larger gains by females than males in empathy. Nonetheless, by the time

they are toddlers, females appear more prosocial, recognizing and willing to help/comfort individuals in distress, and sex/gender difference in empathy continue to be consistent through adolescents and into adulthood. Indeed, twin studies reveal that empathy is largely heritable, consistent with the notion that much variability in empathetic skills is due to genetic causes. In summary, studies in nonhuman animals and younger human populations (infants/children) offer converging evidence that sex differences in empathy have phylogenetic and ontogenetic roots in biology and are not merely cultural byproducts driven by socialization.

The second goal of our review, as described, was to extend our understanding of the phenomenon of empathy itself; namely, whether emotional and cognitive components are independent or related, through surveying neuroimaging and behavioral studies of sex/gender differences in adult humans. In terms of affective empathy, females, compared to men, show higher emotional responsivity and mirroring responses to others' pain, as well as better emotion recognition abilities. Relative to men, females also seem to engage more emotional areas during social cognition. Females also tend to show more prosocial, altruistic behavior as well, which supports the notion that affective empathy drives prosocial behavior. On the other hand, when it comes to cognitive empathy, males seem to show more utilitarian behavior as well as greater recruitment of areas involved in cognitive control and cognition. Evidence regarding ToM is mixed, though it points to differing strategies in how it is implemented between genders and to what ends, which may be underpinned by differences in affective forms of empathy. In general, although there do appear to be sex differences in cognitive empathy, females do not appear to show the same obvious advantage over males, as they do with affective empathy, which may indicate that these systems are somewhat independent.

These behavioral data are consistent with the neurobiological literature showing that different circuits mediate at least two forms of empathy. Affective empathy, compared to cognitive empathy, is more automatic and activates shared motor representation and through neural simulation individuals are capable to understand others' emotions. Part of this affective empathy network involves the mirror neuron system as well as structures belonging to the limbic system, such as the anterior insula and the anterior cingulate cortex. In contrast, a different system supports cognitive aspects of empathy, including perspective taking and mentalizing. This cognitive empathy system includes cingulate, prefrontal, and temporal areas, such as the ventromedial prefrontal cortex, temporoparietal junction, medial temporal lobe, and Brodmann areas 10 and 12 (Zaki and Ochsner, 2012). We reviewed several findings that support this cognitive/affective distinction. Moreover, developmental work and the ethological studies on emotional contagion suggest that the first forms of empathy that emerge are characterized by sharing the same affective states, and by simultaneously activating the same motor programs that control emotions and the visceral responses associated with them. Although the neuroscience literature has little information about brain development, the evidence from psychological and behavioral studies supports the notion that, in females, the basic networks involved in affective empathy are more developed. In contrast, there are few studies comparing males and females in the neural underpinnings of cognitive empathy, so this is an area in which further research is needed. Based on behavioral work, we suspect that sex differences in neural systems responsible for cognitive empathy may not be as great at those for affective empathy.

We also have shown that there are social, contextual, and cultural influences that may foster some of these observed behavioral and neural differences in affective empathy between males and females. Especially in adulthood it seems that males vary more than females in some aspects of emotional processing and altruistic behavior, suggesting that even though it appears that males express less empathy, their higher

discrimination in targeting helping behavior supports the idea that males actually outperform females in their empathetic control. In fact, even in childhood, males appear to have more control over their empathy than females, because, although they are capable of empathy, they exhibit it less automatically. Indeed, examining the different contexts in which males and females differentially exhibit empathy can be quite insightful. For example, males, but not females, are more empathetic towards female targets and targets who they perceive as deserving of help. Females, in contrast, appear more indiscriminately empathetic. Although speculative, it is possible that these sex differences in empathy may be the consequence of different evolutionary selective pressures on males and females, in addition to females' role as primary caretaker, with females exhibiting stronger links between emotional and cognitive empathy (Smith, 2006). For males, increased empathy specifically directed at females may have improved their chances of reproduction, as both sexes prefer mates that are more kind (Li et al., 2002), while decreased affective empathy directed at males may have been adaptive in competitive contexts (Galinsky et al., 2008), such as competing for mates.

While parts of our original questions have begun to be answered, important parts still remain to be clarified. Why and how are males more influenced by contextual factors, such as the qualities of the target (e.g., sex, perceived fairness) and are these effects also present in nonhuman animals and younger individuals? Are sex differences reversed in species in which males are the primary caretakers (i.e., in this case, are males more empathetic than females)? In addition to caring for offspring, are there other evolutionary selective pressures (e.g., sexual selection, competition for mates) have differently shaped empathy in males and females during phylogenesis? Why are disorders of empathy, such as autism and psychopathy, more common in males than females? What are the contributions of early experiences and how do they interact with genetic and epigenetic mechanisms to tune mirror system sensitivities? Are the consequences of empathetic behavior different for males and females? Are the neural underpinnings for cognitive empathy different in males and females, and do females exhibit stronger connections between emotional and cognitive empathy systems?

We propose that a consideration of interindividual differences, and specifically sex/gender differences, can inform our understanding of empathy, including its evolution, the extent to which it is shared with other animals, its development, and its neural underpinnings. Despite the challenges studies of sex/gender differences must overcome (e.g., necessity for large sample size), we think it is worthwhile to explore such differences. Such an understanding may ultimately help to identify and treat disorders of empathy that present sexual dimorphisms, including ASD.

Acknowledgments   Go to: ☑

Footnotes   Go to: ☑

[1]For consistency and simplicity, throughout this review we will refer to sex differences (i.e., biological differences between males and females); however, we also report a number of studies of gender differences (i.e., social differences based on self-identification of participants as men or women). We recognize

that sex and gender each make unique contributions to empathetic skill; however, given that we are including studies of nonhuman animals and infants, it is more parsimonious in these cases to primarily focus on biological individual differences (i.e., sex differences).

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